

SKULL ELEMENTS AND ADDITIONAL REMAINS OF THE PLEISTOCENE BOID SNAKE *WONAMBI NARACOORTENSIS*

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Skeletal remains representing most elements of the large extinct snake *Wonambi naracoortensis* are reported from Pleistocene sediments at Henschke's Quarry Fossil Cave, Naracoorte, South Australia. These specimens include a large number of previously undescribed cranial and post-cranial elements, allowing a fuller description of this poorly known animal. No extant Australasian species compares closely with *Wonambi naracoortensis*, which seems to have been a Gondwanan relic resembling most closely the fossil genus *Madtsoia*, known from South America, Africa and Madagascar. *Wonambi's* skeletal architecture suggests it was adapted for climbing, possibly inhabiting the caves wherein its remains have been found.

□ *Reptilia, Serpentes, Boidae, Wonambi, Pleistocene, South Australia.*

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Henschke's Quarry Fossil Cave consists of a series of small caverns and fissure fills in the Oligocene-Miocene limestones of the Murray Basin (Wells *et al.*, 1984) at Naracoorte, southeastern South Australia (Fig. 1). Several fissures in the area have produced a large quantity and variety of Pleistocene vertebrate remains. One fissure of Henschke's Quarry Fossil Cave, excavated under the direction of the South Australian Museum, contained sediment and fossils accumulated from a natural pit-fall trap (Pledge, 1981).

Subsequent excavations by the author in adjacent fissures yielded some excellently preserved additional material, including associated skeletal elements of the large snake *Wonambi naracoortensis*. The original description (Smith, 1976) was based on eight vertebrae and a jaw fragment. This paper provides the first adequate description of the skull and supplements existing knowledge of the post-cranial elements.

MATERIAL

The remains collected were from two snakes, the more complete being 17% larger than the other. Remains of the larger snake (Fig. 2) were used for the descriptions as they best represented the undescribed elements.

The larger snake (specimen HJD2:84Wi) comprises: left maxilla, anterior part of right maxilla, incomplete left palatine, basioccipital, basisphenoid, left opisthotic-exoccipital, left prootic, fragment of right parietal, left and right dentaries, left surangular, 27 upper thoracic vertebrae, 53 lower thoracic vertebrae, two caudal

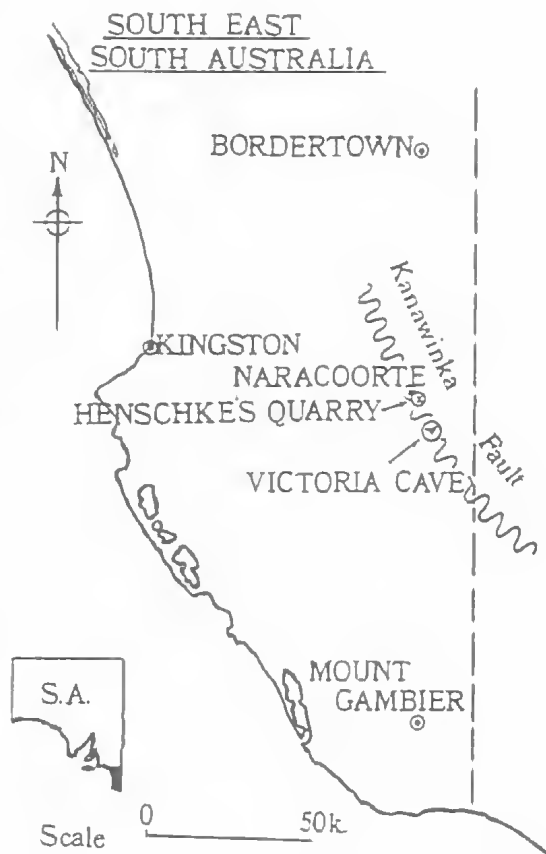


FIG. 1. Locality map, southeastern South Australia.



FIG. 2. The assembled remains of *Wonambi naracoortensis*, specimen number HJD2:84Wi. Length of display 1.5 m.

vertebrae with bifid fixed ribs, seven caudal vertebrae with single fixed ribs (one a fused pair), 152 ribs with rib heads (80 left, 72 right), numerous fragments of rib shafts. Remains of the smaller snake (specimen HJD1:83Wi) comprise: right maxilla, posterior part of parietal, possible pterygoid fragment with seven tooth-sockets, 24 upper thoracic vertebrae, 38 lower thoracic vertebrae, four caudal vertebrae (one with bifid fixed ribs, three with single fixed ribs), 50 ribs with rib heads (30 left, 20 right — including one with fused shaft), numerous fragments of rib shafts. Both specimens are currently in the author's private collection, but arrangements are being made to lodge the larger example (HJD2:84Wi) with the South Australian Museum, Adelaide.

Specimens used in comparisons: SAM R26137, *Python sebae*; SAM unnumbered, *Python* cf. *P. molurus*; SAM R27307 and VM R5850, *P. reticulatus*; SAM R29579, *Boa constrictor*; SAM R26955, *Morelia spilota variegata*; SAM R16053b, *Candoia (Enygrus) australis*; SAM R26966, *Acrochordus arafurae*; BM(NH) 1901-3-29-77, *Trachyboa boulengeri*; AMNH 3154 and BM(NH) R2976, *Madtsoia bai*; SAM R3906, *Liasis olivaceus*; SAM P27777, *Wonambi naracoortensis*. Institutional abbreviations: AMNH, American Museum of Natural History; BM(NH), British Museum (Natural History); SAM, South Australian Museum; VM, Victorian Museum.

Abbreviations (Figs 5-9, 11, 12): a.opht., arteria ophthalmica; ao.vc., anterior opening of vidian canal; ap.l., lateral aperture for recessus scala tympani; ar., articular; ar.co., coronoid articulation; bpt.p., basiptyergoid process; bo., basioccipital; bs., basisphenoid; cen., centrum; cf., costal foramina; c.fr., cerebral foramen; ch.p., choanal process; cid., cid-nerve; de., dentary; e.o., exoccipital; epg?, ectopterygoid?; f?, frontal?; f.jug., foramen jugularis; f.o., fenestra ovalis; lat.w., lateral wing of parietal; lhp., lymphapophysis; l.sf., lingual shelf of dentary; m., maxilla; m.f., mandibular foramen; m.gve., Meckel's groove; n.s., neural spine; oc.c., occipital condyle; op., opisthotic (fused to exoccipital); op.f., optic fenestra; pa., parietal; pg?, pterygoid?; pl., palatine; pm?, premaxilla?; po.vc., posterior opening of vidian canal; poz., postzygapophysis; pro., prootic; prz., prezygapophysis; q?, quadrate?; r.a.p., retroarticular process; s.f.r., single fixed rib; sg.c., sagittal crest; soc., supraoccipital; s.tur., sella turcica; V2, maxillary branch of trigeminal nerve; V3, mandibular branch of trigeminal nerve; VI, abducens nerve; VII, facial nerve; zsp., zygosphene; zyg., zygantrium.

DETAILS OF EXCAVATION

Commercial quarrying exposed the Henschke's Quarry Cave System in the late 1960's. Subsequently the owner discovered a sloping silt bed littered with bones. The South Australian Museum commenced excavations in 1969 and

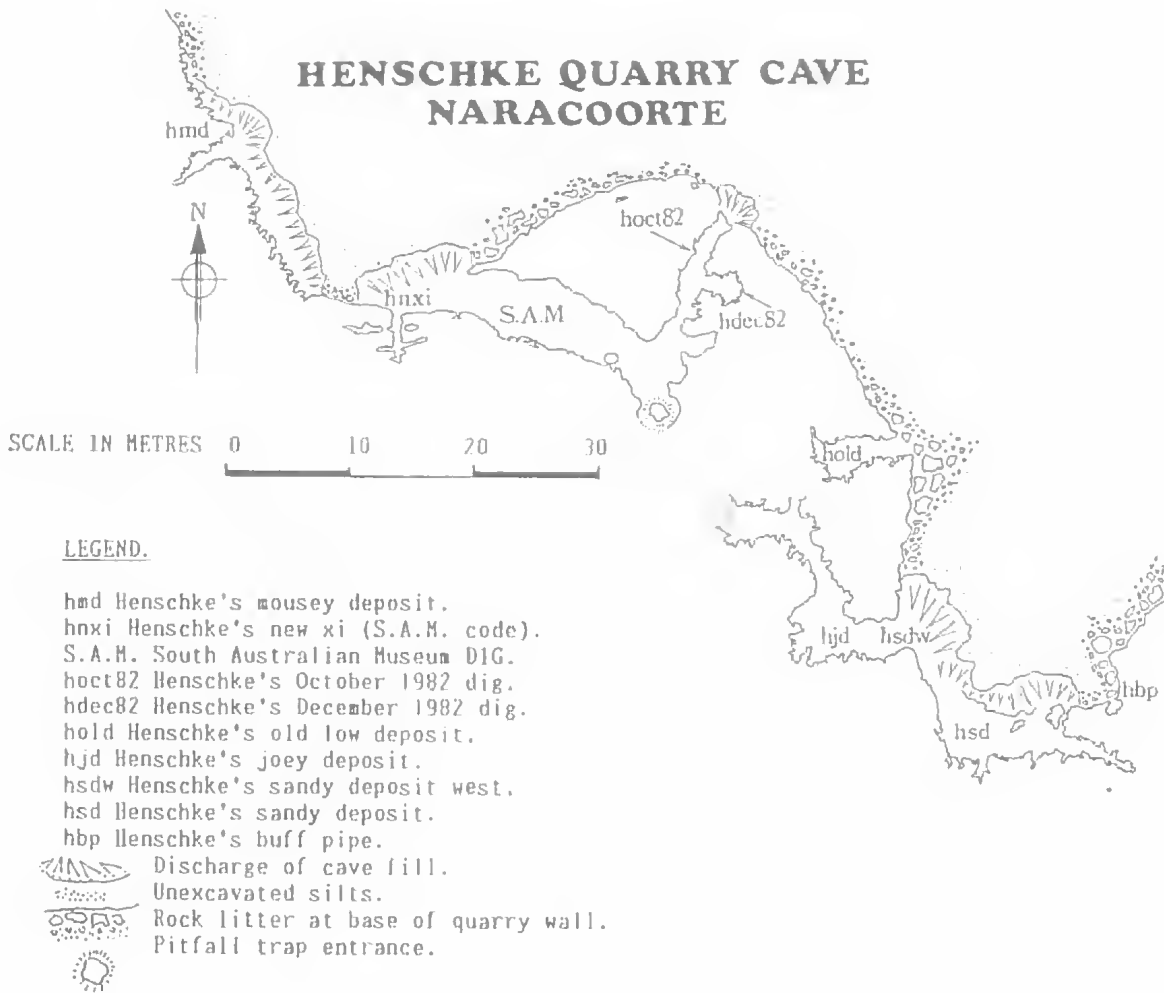


FIG. 3. Plan of fissure excavations at Henschke's Quarry.

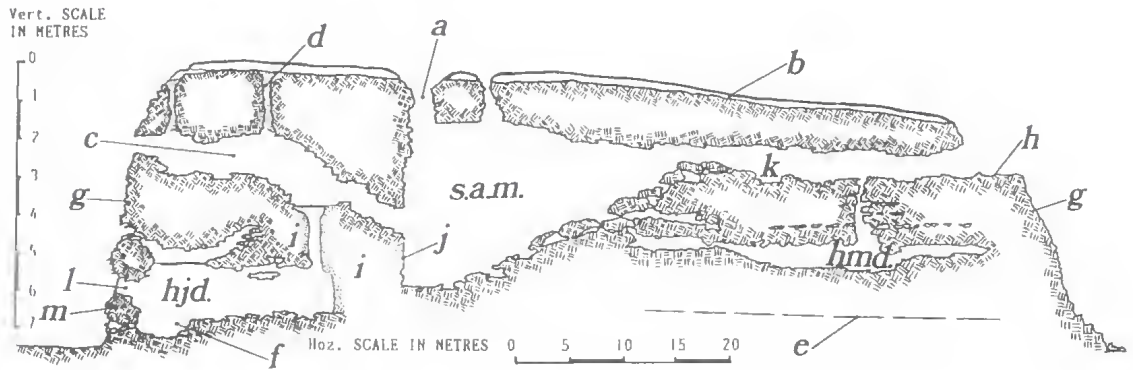
periodically conducted 'digs' up to 1981. After the known fossil-bearing silt had been exhausted, I approached the quarry owner and received permission to continue searching. An exposure of pale sands produced some well-preserved bones, and this was followed along the quarry face to some red silty sediments that yielded the remains of *Wonambi*. Between 1982 and 1986 the fissure coded HJD (Figs 3, 4) was excavated and surveyed. Material removed was recorded in 'dig' lots, and the locations of larger skulls and material from rarer species were plotted onto charts as the dig progressed. Specimens were cleaned, usually washed and dried, then strengthened by immersion in a 10% solution of PVA and water. The venture has been funded by the author, and has occupied more than 8,600 man hours to date.

DESCRIPTION

Cranial and dental features of *Wonambi naracoortensis* are compared to those of other snakes in Table 1.

Maxilla: The maxilla (Figs 5, 6) is 81 mm long, anteriorly robust but considerably reduced in depth and thickness in its posterior two-thirds. A trough passes transversely across the dorsal surface from below the orbit to the lingual side two-thirds from the anterior extremity. The dorsal surface rises to a crest at a point one-third from the anterior, forming an articular surface for the prefrontal. The posterior end shows a small area for articulation with the ectopterygoid. Five small foramina of roughly equal size penetrate the maxilla between the anterior tip and the orbit.

There are 22 tooth sites in the maxilla, with



CROSS-SECTION ALONG FISSIONS

FIG. 4. Cross-section along cave system at Henschke's Quarry.

Abbreviations: a. entrance to pit-fall trap over main cavern; b. Terra rossa soil profile; c. cavern investigated by SAM (no evidence of bones); d. solution tube filled with Pliocene Parilla Sands; e. interface between harder Naracoorte Limestone Member and the softer underlying bryozoal sequences of the Gambier Limestone; f. lowest extent of deposit, produced remains of *Wonambi*; g. quarry faces; h. bench level at quarry exposing entrance to k; hjd. deposit excavated by the author 1982-1986; hmd. deposit excavated by the author 1982-1986 (contained only extant species in upper levels); i. material unexcavated due to hazardous conditions; j. hard calcified clay plugging lower deposit; k. shallow cavern leading to the bone bed in s.a.m.; l. entrance to hjd exposed by digging away quarry debris; m. fallen boulders; s.a.m. cavern excavated by SAM 1969-1981.

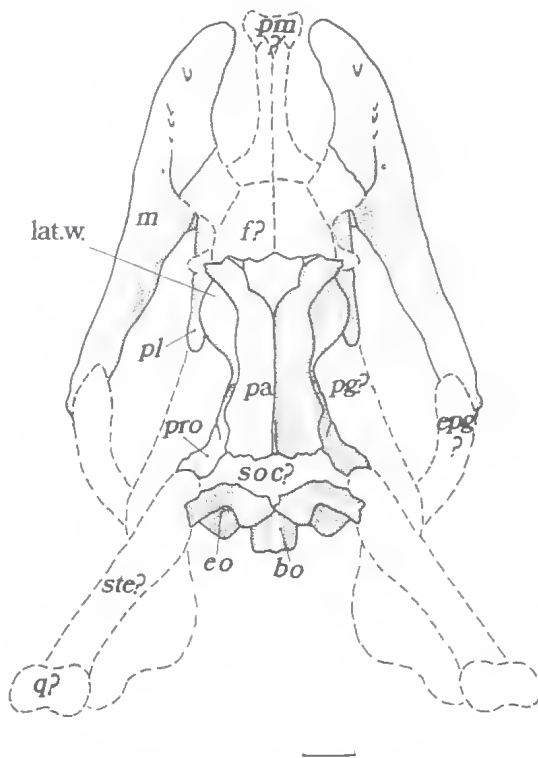


FIG. 5. *Wonambi naracoortensis*, skull in dorsal view; scale bar 1 cm.

functional teeth approximately alternating with developing replacement teeth (lost from this specimen). The conical teeth are of typical boid-like form and are directed posteriorly at approximately 45° to horizontal. The anterior teeth show a slight reverse curvature and cutting edge (Frazetta, 1966); the posterior teeth are smaller and point lingually at approximately 45°, as well as posteriorly. The teeth are smaller and more numerous than in any other species examined in this study (Table 1).

Palatine: The body of the palatine (Fig. 6) is broad and rather flat. The lateral maxillary process is damaged, but the primitive choanal process (Underwood, 1976) is well developed and forms a sub-circular perforation as it approaches the anterior end of the tooth row. The anterior articular surface of the choanal process is thickened and contains a hollow with a foramen at its base. A small foramen is also present in the antero-dorsal surface of the choanal process, just behind its widest point. A ridge crosses the ventral surface of the lateral process, commencing against the anterior end of the tooth row and curving away from it posteriorly. The anterior part of this ridge defines the lingual side of the sub-circular perforation. Posteriorly the ridge diminishes at the widest extent of the palatine. The articulation with the pterygoid is indicated by a notch between the posterior end of the tooth row and the rear part of

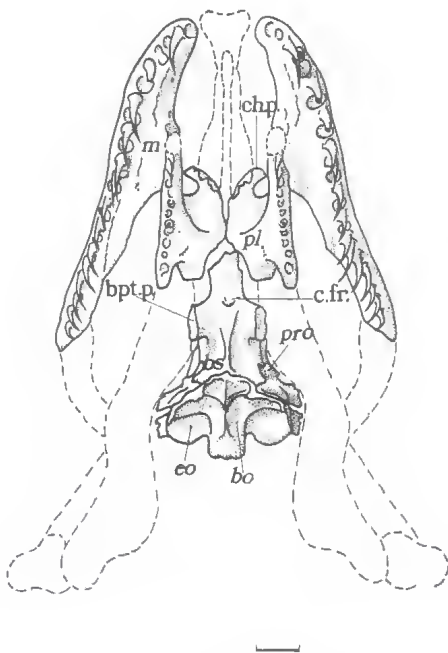


FIG. 6. *Wonambi naracoortensis*, skull in ventral view;

the lateral process. The extreme anterior end of the tooth row is missing; there was possibly one more tooth site in addition to the 12 preserved. The small and close-set teeth are directed posteriorly and curve back sharply to lie at about 30° to the horizontal. The proportional width of the palatine is exceeded only in *Acrochordus arafuræ* (SAM R26966). In its general form the palatine is matched most closely in the tropidophids *Tropidophis taczanowski* (Underwood, 1976) and *Trachyboa boulengeri*, while the number of teeth is approached most closely in *Acrochordus arafuræ* (9 teeth).

Dentary: The dentary (Fig. 7) is dorso-ventrally compressed and broad. It achieves its greatest depth at the facet for articulation with the complex of other bones forming the lower jaw. The facet extends for approximately 44% of the length of the dentary. Meckel's groove is deep and broad, tapering anteriorly, and is open to the tip of the dentary. The missing splenial would fit along its inswept postero-ventral surface. One small foramen is situated beneath tooth sites 6 and 7. There are 25 sites for teeth, including vacant sites for developing replacement teeth (not preserved).

TABLE 1. Comparisons of cranial elements. All linear dimensions are scaled to uniform maxilla length (84 mm) in *Python reticulatus* (SAM R27307). The few measurements available for *Madtsoia* are: no. of tooth sockets, dentary, 9+; dentary foramina, adjacent to teeth, 3.8; number of foramina (dentary), 3 (all of these measurements for *M. bai*, British Museum (Nat. Hist.) R2976); and angle of zygapophyses, 22° (*M. bai*, AMNH 3154), and 20° (*M. madagascariensis*, after Hoffstetter, 1959). Paracotylar foramina are present in both species.

	<i>Wonambi naracoortensis</i>	<i>Trachyboa boulengeri</i>	<i>Candoia australis</i>	<i>Acrochordus arafuræ</i>	<i>Constrictor constrictor</i>	<i>Python sebae</i>	<i>Python molurus</i>	<i>Python reticulatus</i>	<i>Python reticulatus</i>	<i>Morelia spilota</i>	<i>Liasis olivaceus</i>
Scaling Factor	1.04	11.66	6.46	5.49	2.79	3.56	2.22	1.00	0.91	3.23	2.13
Maxilla length	84	84	84	84	84	84	84	84	84	84	84
Dentary length	78.3	112	87.88	91.1	82.3	79	85.3	83.4	81.5	80.4	74
Mid-Dentary width	14.9	18.7	6.46	8.8	8.4	10.7	16.2	13.3	13.1	7.4	8.5
Basioccipital width	27.4	37.3	30.37	35.7	26	28.1	27.8	27.8	25	23.14	30.7
Basioccipital length	24	31.5	26.49	23.1	21.8	23.1	25.1	25.1	15.3	13.7	23.9
Basipterygoid width	17.8	26.8	27.1	23.1	27.9	23.1	24.4	24.4	17.5	14.9	24.2
Distance Basipterygoid to Condyle	40.4	61.9	64	42.8	43.5	48	48.9	36.1	32.1	46.8	43.7
Width of Palatine	17.3	14.0	9.69	19.8	10.3	9.3	8.7	—	6.3	6.8	7.0
Surangular width	12.1	17.5	9.1	8.2	19.5	9.6	12	8.4	8.6	8.1	6.6
Surangular length	88.3	154	102.7	128.5	91.2	87.2	98.4	94.8	94	97.9	85.5
Surangular height	6.5	31.5	19.4	8.8	20.1	18.2	28.4	22.2	25.2	25.8	21.3
Articular width	9.6	19.8	10.34	20.9	10.3	7.8	14	13.4	13.5	12.3	9.4
Articular height	10.1	10.5	7.75	19.2	10.9	8.9	14	15	15.4	12.9	8.3
Length Mandibular Fenestra	17.8	22.2	31	15.4	9.8	24.9	31.1	4.2	5.7	11.3	5.8
Width Mandibular Fenestra	2.1	3.5	6.5	5.4	2.2	3.9	6.2	3	3.2	5.5	2.1
TEETH SIZE											
Maximum length Dentary	9	14	21.9	17	17.9	12.5	16.7	16	16.5	16.8	15.1
Minimum length Dentary	4.2	3.5	4.5	9.9	4.2	4.3	5.6	6.3	6.2	4.2	4.7
Maximum length Maxilla	9.4	14	20	18.1	16.5	13.9	15.6	18	16.3	16.2	15.8
Minimum length Maxilla	4.4	8.2	5.2	8.8	4.2	4.3	7.1	6.3	6.4	3.2	4.3
NO. OF TOOTH SOCKETS											
Maxilla	22	16	18	20	19	17	19	17	17	17	19
Palatine	12+	7	6	9	5	7	6	7	7	5	6
Dentary	25	21	18	17	18	18	20	16	16	19	19
Pterygoid	—	16	10	13	12	8	10	9	11	9	11
FORAMINA											
Dentary adjacent teeth	6-7	5-6	5-6	5-6	6-7	5	4-5	4-5	4	4	4-5
Number of Foramina	1	1	1	2	1	1	1	1	1	1	1
Maxilla adjacent teeth	5-9	—	4-5	9-12	5-6	4-6	4-9	4-5	3-6	4-5	3-4
Number of Foramina	5	0	2	2	2	3	3	3	3	1	2
Angle of Zygapophyses	22°	—	3°	0°	0°	3°	9°	3°	3°	10°	3°
Presence of Paracotylar Foramina	Y	Y	Y	Y	Y	N	N	N	N	N	N

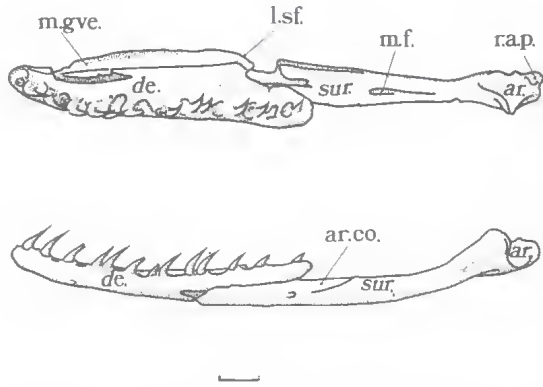


FIG. 7. *Wonambi naracoortensis*, left mandible in dorsal view (above) and lateral view (below); scale bar 1 cm.

The conical teeth are directed posteriorly along the dentary at approximately 45° to horizontal; the hindmost ones are directed lingually at almost 60° to the axis of the dentary.

Wonambi naracoortensis has numerous (25) tooth sites, and of the species examined only *Trachyboa boulengeri* (21 tooth sites) approaches *Wonambi* in this respect. The dentary resembles that of *Madtsoia*, as described Hoffstetter (1959), in the form of the lingual shelf along the ventral surface, although it is even more pronounced in *Wonambi*. However, *Madtsoia* has three prominent fossae on the external surface of the dentary, compared to *Wonambi*'s single small one, and *Madtsoia* has only nine tooth sites anterior to the articulation for the surangular whereas *Wonambi* has 15 tooth sites.

Surangular: The surangular (Fig. 7) is wider than high and lacks a coronoid process. The mandibular foramen is a small channel in the otherwise rather flat dorsal surface, and it extends forwards

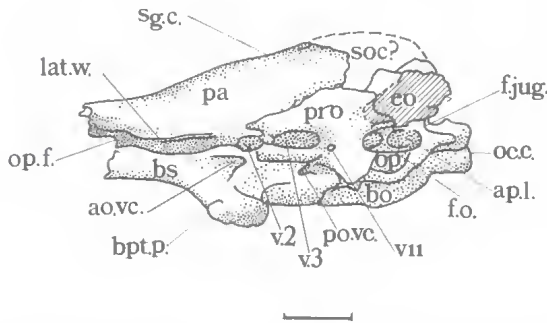


FIG. 8. *Wonambi naracoortensis*, brain-case in left lateral view; hatching indicates articular surface for supratemporal; scale bar 1 cm.

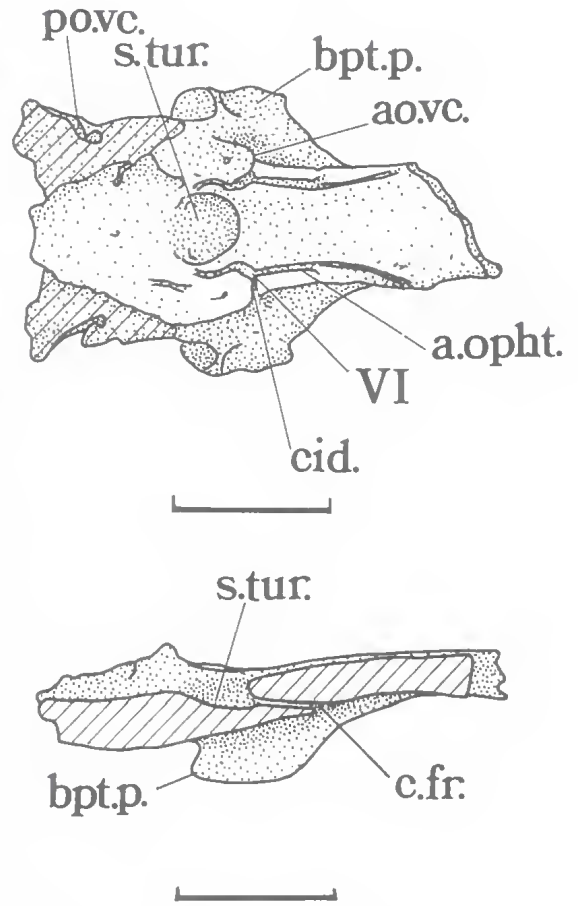


FIG. 9. *Wonambi naracoortensis*, basisphenoid in dorsal view (above) and sagittal view (below); hatching indicates articular surface for prootic; scale bar 1 cm.

approximately half-way from the articular. The articulation with the dentary doubtless allowed some flexion, since the broad, flat antero-ventral surface fitted loosely into the cleft at the posterior end of the dentary. An ascending ridge articulates with a corresponding groove in the dentary. This ridge-and-groove articulation would serve to keep the two elements aligned during flexion. Anteriorly the lingual surface has a groove that aligns with Meckel's groove in the dentary. Just forward of the articular surface for the quadrate, the surangular is almost circular in cross-section. The surface of the articular is saddle-shaped and extends obliquely across the surangular (lingual side forward) at almost 60° to the axis of the jaw.

By comparison with the other species examined, *W. naracoortensis* has a surangular that is shorter

than average, though its maximum width is unexceptional. The lack of a coronoid process is shared with *Acrochordus arafurae*; all other specimens examined possessed a prominent coronoid process.

Basioccipital: The basioccipital (Figs 5, 6, 8) forms the ventral and major part of the occipital condyle. The ventral surface is strongly keeled. A slight transverse ridge extends from the keel's most ventral point to a process along the junction with the prootic. The basioccipital is widest at the speno-occipital process for the insertion of hypaxial neck muscles. This is at the junction with the prootic/opisthotic, beneath the vestibular fenestra (Rieppel, 1979) into which the stapes would penetrate. The proportions of the basioccipital are matched in the other species examined.

Basisphenoid: Immediately anterior to the basioccipital, the basisphenoid (Figs 6, 8, 9) forms a continuation of the underside of the brain-case. Its upper surface has a prominent sella turcica, between the anterior openings of the vidian canals which are exposed on the outer surface of the basisphenoid above the prominent basipterygoid processes. From the sella turcica a small oval cerebral foramen is directed antero-ventrally. This foramen exits on the ventral surface just anterior to the basipterygoid processes. The keel below the basioccipital continues forwards on to the underside of the basisphenoid. This keel flattens between the basipterygoid processes and bifurcates to enclose the cerebral foramen. On the mid-dorsal margin of the basisphenoid, foramina occur at the junction with the prootic, possibly for nerve V₂. The highly-developed basipterygoid processes point outwards, downwards and posteriorly. The articulation with the pterygoid is sub-triangular, with the apex of the triangle rising as a ridge to meet the brain-case at the anterior extremity of the prootic. Just in front of this rising ridge is the anterior opening of the vidian canal (Underwood, 1976). The posterior opening of the vidian canal exits at the back of the basipterygoid processes, at the junction with the prootic. The anterior end of the basisphenoid, the basi-parasphenoid (Underwood, 1976), is missing from this specimen. The basisphenoid ends in a rather solid, flat rectangular section, representing the broad base of the cultriform process. The ventral surface exhibits a slight ridge anterior to the cerebral foramen.

A distinctive and undoubtedly primitive feature is the cerebral foramen, which is shared only with *Trachyboa boulengeri* among the specimens examined. The basipterygoid processes are as

highly developed as in any of those specimens. Both left and right vidian canals are of similar size in *Wonambi*.

Opisthotic-Exoccipital: The opisthotics and exoccipitals (Figs 5, 6, 8) are fused. The exoccipitals form the upper and smaller portions of the occipital condyle and are hollowed posteriorly to allow flexion of the atlas vertebra at the condyle. In this hollow is the jugular foramen for nerves IX, X, XI and three smaller hypoglossal foramina for nerve XII. The anterior margin forms the rear wall of the fenestra ovalis. Inside the vestibular fenestra, which should be encased by the crista circumfenestralis, is the lateral aperture of the recessus scala tympani. The posterior margins of the exoccipitals form almost the entire foramen magnum. Their contact above the foramen is at best minimal, but minor damage may have reduced this slightly. This contact appears to be even less than in *Dinilysia patagonica* (Rieppel, 1979, after Estes *et al.*, 1970), which is the most ancient snake skull described to date. The apparent lack of a crista circumfenestralis and the minimal contact between the exoccipitals above the foramen magnum are both primitive features matched in *Dinilysia* and close to the conditions in lizards (Rieppel, 1979).

Prootic: The prootic (Figs 5, 6, 8) is an irregular element partially encasing the side of the brain cavity. It articulates with the dorsal edges of the basioccipital and basisphenoid, and lies anterior to the opisthotic-exoccipital and posterior to the lower margin of the parietal. Anteriorly it contributes to the margin of the foramen for nerve V₂. Behind this are the larger foramen for nerve V₃ and a smaller one for VII. Other tiny foramina are present, one of which would be for V₄. The posterior edge of the prootic forms the margin of the fenestra ovalis in the vestibular fenestra. This should be enclosed by the crista circumfenestralis, which is illustrated by Rieppel (1979) as a bubble-like structure penetrated by the stapes. However, there is no evidence of this structure on any of the associated elements. It is also noteworthy that the genus *Acrochordus* is recorded as lacking a crista circumfenestralis (McDowell, 1975) or, at best, as having it highly modified (Rieppel, 1979).

Parietal: An anterior fragment of the right parietal of specimen HJD2:84Wi (Figs 5, 8) contacts the basisphenoid and encases the anterior dorsal surface of the brain. A near-complete parietal (SAM P27777), identified from the Victoria Fossil Cave, also near Naracoorte (Fig. 1), is used to supplement the description. This

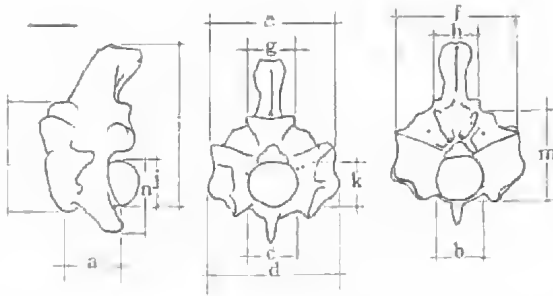


FIG. 10. Measurements of vertebrae. Example shown is an upper mid-thoracic vertebra with prominent hypapophysis and three paracotylar foramina; scale bar 1 cm. Measurements: a, length, condyle to cotyle, measured ventrally; b, condyle width; c, cotyle width; d, width across diapophyses; e, width across prezygapophyses; f, width across postzygapophyses; g, zygosphene width; h, zygantrum width; i, height, from ventral margin of condyle to crest of neural spine; j, condyle height; k, cotyle height; l, height, from zygosphene to base of cotyle; m, height, from dorsal margin of condyle to tip of hypapophysis.

near-complete parietal was from a smaller individual and has been enlarged proportionally in reconstructing the skull.

Anteriorly the parietal has a well-formed sagittal crest and is rather slender overall, having only a slight swelling centrally. Its overlapping articulation with the supraoccipital has the form of an inverted 'V'. The front part of the parietal is nearly flat on the dorsal surface, and the articulation with the frontals is irregular. The parietal overlaps the frontals for most of its width and is overlapped, possibly by the post-frontals, at the outer surfaces. An indication of the optic foramen is present on the lower anterior sides,

enclosed within the parietal, frontal and (possibly) basi-parasphenoid. Above this a rounded, slightly downturned wing extends posteriorly past mid-length of the parietal. This feature has not been observed on any other specimen examined. A small projection pointing posteriorly contacts the prootic at the foramen for the nerve V_2 . The ventral edge of this foramen appears to be formed by contact with the basisphenoid, though slight damage to the prootic may have removed an extension that completed the foramen.

Pterygoid: A thin, flat and quite broad fragment containing seven tooth sites appears to be part of the pterygoid. While its margins are damaged, so that its orientation is in doubt, the remains of an articular surface probably represents the articulation with the basiptyergoid process. The presumed anterior part of the tooth row is curved, unlike all other specimens examined. The tooth sockets are smaller than those in the palatine and very close-set, which suggests the pterygoid may have contained numerous teeth. Such an arrangement would be consistent with the other tooth-bearing elements of *W. naracoortensis*.

Vertebrae: Comparisons with the eight thoracic vertebrae described by Smith (1976), and additional vertebrae since obtained from the Victoria Fossil Cave, confirm that the material collected does represent *Wonambi naracoortensis*.

The vertebrae have broad paradiapophyses, high neural spines that slope posteriorly, and possess variable numbers of small paracotylar foramina (none to three per vertebra). The vertebrae were initially sorted into body regions following Simpson (1933). The anterior thoracic vertebrae are identified by the presence of hypapophyses. Posterior thoracic vertebrae are similar in form, but lack hypapophyses. Anterior caudal vertebrae

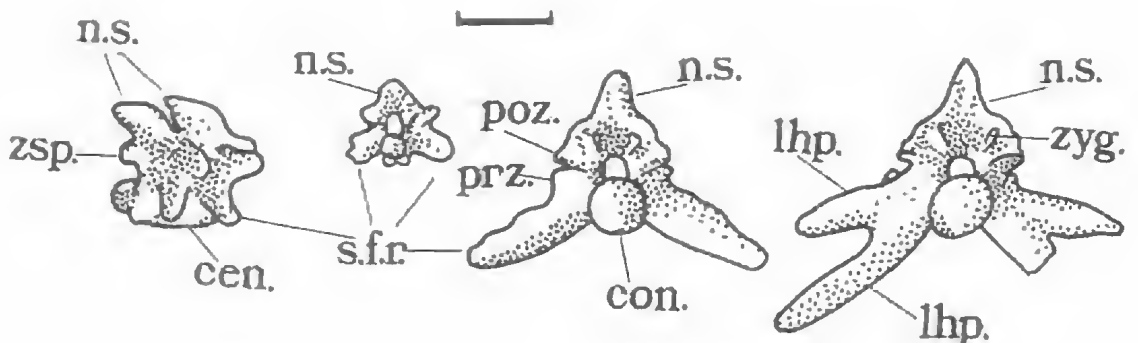


FIG. 11. *Wonambi naracoortensis*, variations in caudal vertebrae; scale bar 1 cm.

(Fig. 11) have bifid diapophyses (or fused ribs) which were termed lymphapophyses by Romer (1956) since they house the lymph hearts. These vertebrae are of limited number, never more than ten (Simpson, 1933). Finally there are the posterior caudal vertebrae (Fig. 11), with single fixed ribs. One of these is a fused pair, a feature seen in other snakes examined. The posterior caudal vertebrae are much more numerous than the anterior caudals, varying from 15 to 92 in species tabulated by Simpson (1933).

The newly-collected vertebrae were derived from two individual snakes — 89 from a large individual and 66 from a smaller one. Where possible, 14 measurements were taken of each vertebra, using dial calipers (Fig. 10). Many vertebrae were damaged by the mechanics of excavation, as well as from the apparent activities of termites. Nevertheless, damaged vertebrae could often be measured from the sagittal plane, thus giving a half-value which could then be doubled to provide measurements such as maximum width across paradiapophyses. These numerous measurements allowed even small fragments to be plotted in sequence; thus it proved possible to estimate the

maximum number of vertebrae and, hence, *Wonambi's* body length.

The 14 measurements were plotted on slips of paper in distinctive colour codes; by aligning these slips adjacent to each other it was possible to establish the correct sequence of vertebrae in the snake. All the resulting data are lodged with the South Australian Museum.

On examining the resulting sequence of anterior thoracic vertebrae, it was noticed that some had hypapophyses and others did not. All those vertebrae without hypapophyses transpired to be from a location one to two metres away from the major accumulation. The colour-coded slips representing vertebrae from that second locality were removed. Both sets of slips when placed in sequence, presented a neat progression of dimensions, revealing that the material comprised the remains of two snakes. The conspecificity of the two individuals was illustrated simply by graphing the dimensions of the smaller animal's vertebrae on to an elastic strip and stretching it to the same size as the larger specimen. All dimensions matched when the elastic was stretched uniformly.

The slips were also spaced to conform with a graph which approximated the contours of the

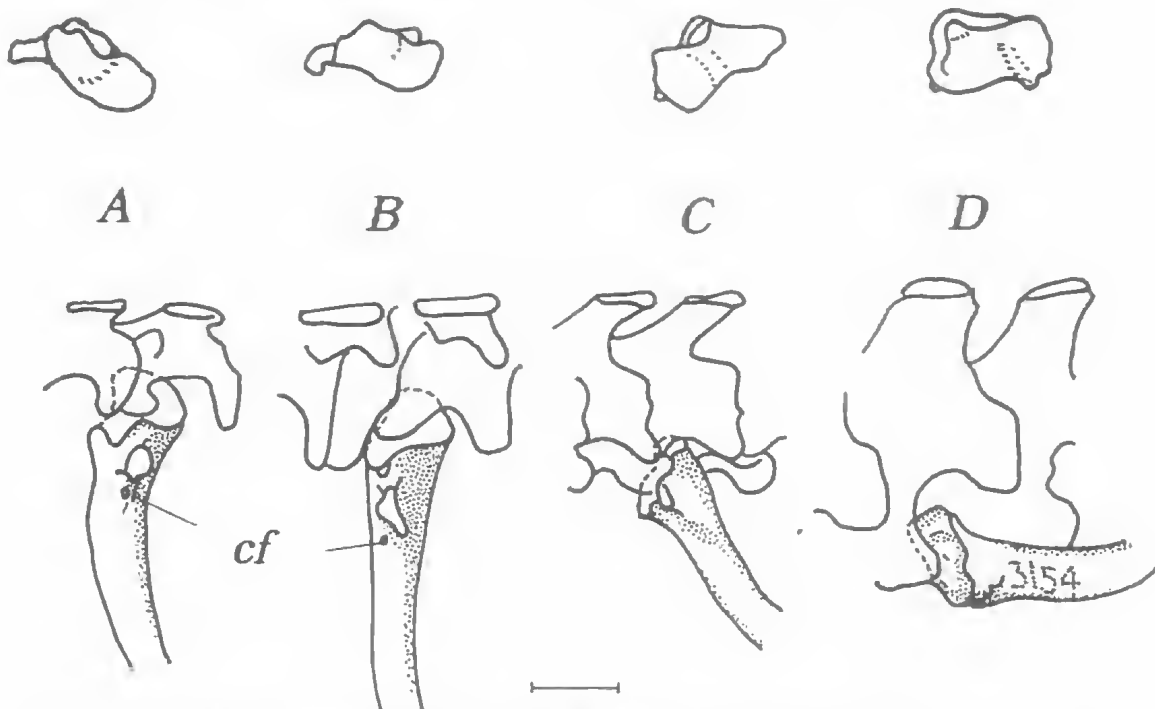


FIG. 12. Rib heads, in proximal view (above), and their articulations in postero-dorsal view (below); scale bar 1 cm. A, *Python molurus*; B, *P. reticulatus*; C, *Wonambi naracoortensis*; D, *Madtsia bai*.

modern boid — *Morelia spilota variegata* (SAM R26955). On this extant specimen the width of every fifth vertebra was measured. The data were graphed to compare with the graphs of *Wonambi*. This exercise revealed remarkable similarity in general form, although some significant gaps were evident in the *Wonambi* sequence. The slips of specimens showing termite damage were noted. This form of damage was limited to the larger sequence of vertebrae and coincided mainly with the margins of missing sections.

From these comparisons it was concluded that *W. naracoortensis* probably had between 350 and 400 vertebrae. This certainly lies within boid limits tabulated by Rochebrune (cited by Simpson, 1933).

The average length for a vertebra is 14.2 mm. Adding a nominal 0.5 mm to each vertebra for cartilage, 140 mm for cranium and cervicals and an estimated 100 mm for extreme posterior caudals, it was calculated that *Wonambi* was between 5.39 metres and 6.13 metres in total length.

Ribs: Most of the ribs were damaged in the same way as the vertebrae. An attempt to arrange the ribs in sequence, using measurements from the head and shaft, proved fruitless because there was too little variation from one rib to the next.

The free ribs are holocephalous, although the rib head is partly divided, (a slightly concave portion, a ridge then the adjacent cupped dorsal area). The articulation is with the large, prominent paradiapophysis (Smith, 1976) anteriorly placed at each side of the centrum. The shaft is steadily curved, the distal extremity ending in a cylindrical shaft with a cup-shaped termination for attachment of the cartilaginous connection of the ventral scutes. The proximal end of the shaft is more ovoid in cross-section. The anterior ribs exhibit an expanded costal process for the attachment of muscles (Fig. 12). *Python reticulatus* and *P. molurus* present a well-developed costal process, extending from the dorsal cupped area. In *Wonambi* the costal process is not as conspicuous because the rib head sweeps gently to its tip. The process would, in fact, be much more robust than in the pythons examined, but less so than *Madtsioia bai*. Both *P. reticulatus* and *P. molurus* exhibit a large foramen at the base of the costal process whereas *P. molurus* exhibits several smaller foramina posterior to it. None of these is evident in *Wonambi*.

In *Wonambi* the lymphapophyses of the caudal vertebrae are very solid, the upper ramus extending almost horizontally and the lower slanting at approximately 30° below the horizontal. They contrast with the fine, flattened and down-turned

lymphapophyses of *P. molurus*. The bifid ribs of *M. spilota variegata* are much more like those of *Wonambi* but are unproportionally smaller in size.

DISCUSSION

Wonambi was a large, heavy-bodied snake, though its skull, teeth and anterior vertebrae are relatively small and delicate. A 6 metre individual with a diameter of about 250 mm and a girth of about 800 mm could have weighed 250 kg. The skull is dorso-ventrally compressed and the orbits are set well forward. The lower jaw is very lightly constructed, the nearest comparison being with *Acrochordus*, an aquatic species. On the lower thoracic vertebrae the angled zygapophyses of *Wonambi* resemble those of *Madtsioia*. The longest extant snake, *Python reticulatus*, has almost horizontal zygapophyses inclined at only 3°; those of *Python molurus* (Indian Rock Python) are inclined at about 10°, compared to *Wonambi* and *Madtsioia* inclined at about 20-22°. The inclination of zygapophyses is discussed by Romer (1956), and in general terms the greater the inclination the greater is the constraint on lateral flexion. In snakes this restricts one major means of locomotion, lateral undulation, but it increases the ability for vertical flexion. The tall neural spines provide anchorage for muscles having greater mechanical advantage than those in snakes having low neural spines. Similarly the prominent paradiapophyses provided a good anchorage for the ribs and their associated muscles; narrower attachment to the vertebrae would lessen the mechanical advantage of the associated muscles. The advantage achieved with broad paradiapophyses may have outweighed the limitation resulting from steeply-inclined zygapophyses.

Wonambi was too bulky to have been an arboreal snake, although its climbing ability may have been reasonably good — a necessary requirement if it occupied caves. It is possible that *Wonambi* had feeding habits similar to those of *Acrochordus*, fish being available in the lagoons of its habitat. Large prey capable of struggling vigorously are unlikely to have been taken, since *Wonambi's* jaws were rather weak. The reduction in lateral flexion would limit its ability to constrict animals, thus implying that it subsisted mainly on small prey.

Wonambi's remains were found in the lowest portion of the deposit, an area of horizontally-banded sediments, gritty sands alternating with red silts. The bedding inclined steeply along the side furthest from the entrance through which it must have accumulated. This

bedding pattern was consistent with the formation of a miniature delta, with sediment washing into a cave-pond and forming an inclined bank in deeper water. Evidently the cave contained water that would have been attractive to snakes. If the water was permanent, the age of the deposit is likely to coincide with a higher water-table and a closer coastline, possibly over 100,000 years ago (Schwebel, 1983). This is consistent with recent dating of the Victoria Fossil Cave (Veeh, unpublished) and also with similarities in the faunas of the two deposits. Snakes, particularly large ones, are very dependent on water, so it is likely that increasing aridity across the continent placed considerable pressure on the population of large snakes, possibly leading to their extinction. How such large snakes survived so long in temperate conditions remains a mystery.

In her original description Smith (1976) compared the vertebrae of *Wonambi* to those of the genus *Madtsioia*. Both share the back-sloping neural spine, broad paradiapophyses, paracotylar foramina and the lack of accessory processes. *Madtsioia* (Hoffstetter, 1959) also shares the inswept lingual shelf on the underside of the dentary and Meckel's groove being open to the tip.

Wonambi's primitive nature is also evident when it is compared to other species known to possess plesiomorphic character states. Paracotylar foramina (Underwood, 1976) are shared with the extant Tropidophinae, *Bolyeria*, *Casarea*, *Candoia*, *Boa*, *Acrochordus*, and the fossil genera *Madtsioia* and *Gigantophis*. A well-developed choanal process (Underwood, 1976) is shared with some members of the same group. The small contact between the exoccipitals is shared with the fossil *Dinilysia patagonica* (Rieppel, 1979). The apparent lack of a crista circumfenestralis is shared with *Dinilysia* and, less certainly, with the Acrochordidae (McDowell, 1975). The *Acrochordus* specimen I examined (*Acrochordus arafurae*, SAM R26966) certainly appears to have a crista of some form.

Wonambi's ribs, hitherto undescribed, appear intermediate between those of *Madtsioia* and those of the pythons. They are generally heavier in structure than the ribs of pythons and show no evidence of the costal foramina seen in some extant species (e.g. *Python molurus* and *P. reticulatus*). Underwood's (1976) phyletic analysis indicates that the Pythoninae examined (*Python*, *Liasis* and *Morella*) are similarly separated from the Boini. Pythons are a more homogeneous group in almost all features examined. Since *Wonambi* does not seem to be closely related to pythons I have

concentrated on comparisons with those of the Boini possessing paracotylar foramina. Underwood's first group includes *Casarea*, *Bolyeria* and the Tropidophinae. These are differentiated from other boids by the hyoid cornua being parallel, the absence of pelvic spurs from females, the left lung being reduced, and a terminal entry of the trachea into the lungs. These features cannot be determined in *Wonambi*'s fossil remains, but *Wonambi* shares the primitive choanal process and cerebral foramina with some members of the Tropidophinae. The second group includes *Candoia* (*Enygrus*), *Boa* and the fossil snakes *Madtsioia* and *Gigantophis*.

Underwood's (1976) phenetic analysis also clusters the pythons, species possessing paracotylar foramina are grouped, *Bolyeria*, *Casarea*, and the Tropidophinae. The one exception is *Boa*, and that does not appear to have close affinities with *Wonambi*.

Rage (1982) illustrates the phylogenetic relationship of snakes, clustering *Dinilysia*, *Xenopeltis*, *Boa*, *Paleophis*, *Nigerophoides* and *Acrochordus*. He suggests that the elapids, colubrids and vipers evolved from ancestral stock among the Acrochordidae, subsequently dispersing in the Eocene and Oligocene. He illustrates the possible migration routes from Laurasia to Australia, Africa and South America in the Miocene. Rage also considered the earlier radiation of snakes from Gondwanaland during the Cretaceous, which may have entailed migrations by the descendants of *Madtsioia*. *Wonambi*, only recently extinct, represents a diverse group of Gondwanan survivors, several of which (*Candoia*, *Casarea*, *Bolyeria* and *Tropidophis*) have remained isolated from suspected migration routes (Fig. 13).

The absence of extant Australasian species sharing plesiomorphic character states with *Wonambi*, excepting perhaps *Candoia* and *Acrochordus*, has been established. Immunodiffusion studies of plasma transferins in extant Australasian elapids (Schwaner *et al.*, 1985), reveal an affinity to the Asian snakes. Microcomplement fixation data suggest a date of about 20 My for the separation between Australasian and Asian/African elapids. Australia must have made sufficient contact with Asia for a successful migration of snakes to take place at that time.

A Miocene migration to Australia raises the question of a land bridge extending to Asia some 20 My ago. If this were relatively unbroken one would expect more successful migrations, both to



FIG. 13. Distribution of Gondwanan boids related to continental geography of the Late Cretaceous (after Rage, 1982). Fossil forms: d, *Dinilysia*; g, *Gigantophis*; m, *Madtsoia*; w, *Wonambi*. The following extant Gondwanan relicts, showing some affinities with *Wonambi*, remain isolated from suspected post-Cretaceous migration routes: a, *Acrochordus*; b, *Bolyeria*; c, *Casarea*; e, *Candoia* (*Enygrus*). Arrows indicate possible migration routes in the Mesozoic.

and from Asia. The evidence of faunal exchanges in the Miocene is meagre, but a one-way transfer (Australian marsupials did not establish themselves in Asia), is possibly the result of the progression of a land bridge, the Asian end disconnecting before the insular population reached Australia. This would have selectively limited the species en route from Asia, and prevented any return. If elapids arrived in Australia 20 My ago it is likely that other creatures, perhaps including the pythons, would have arrived at the same time.

Wonambi's closest affinity is undoubtedly with *Madtsoia*. Being a Gondwanan species of wide distribution it is likely that the genus *Madtsoia* radiated beyond Gondwanaland as migration routes opened up into the northern hemisphere. *Wonambi* lingered on in the isolated Australian land mass as *Madtsoia's* descendants evolved elsewhere to produce, among others, the pythons. Some of the pythons arrived in Australia during the Miocene, representing the ancestral stock of the extant species. *Wonambi* survived well into the Pleistocene, to become extinct along with much of the Australian megafauna. It is truly a ghost from the past that we have just missed seeing alive.

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